**ANOPLODACTYLUS PETIOLATUS (PYCNOGONIDA)**

**AND HYDRACTINIA ECHINATA (HYDROZOA) – OBSERVATIONS ON GALLS, FEEDING BEHAVIOUR AND THE HOST’S DEFENCE**

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ABSTRACT. – Observations and experiments are reported on the relationships between *Anoplodactylus petiolatus* and its prey, *Hydractinia echinata*, with special reference to feeding, movement and avoidance of the colony’s defence. The latter includes active elements (usage of proboscis and legs) as well as a kind of immunity: Even after having been engorged, *Anoplodactylus* can successfully withdraw from the gastric cavity without serious bleeding. In addition, we have documented living *Anoplodactylus* larvae within polyps transformed to “gallzooids”.

**INTRODUCTION**

A few members of the Pycnogonida, an ancient group of marine arthropods, have been found to feed on or encyst larvae in cnidarian polyps (see reviews in Helfer & Schlottke 1935, Wyer & King 1974, Staples & Watson 1987), i.e. animals that in their nematocysts possess a highly effective defence system which comparatively few animals are able to overcome, whether to use the colonies only as hiding places, e.g. clownfish and anemone shrimps, or to prey on them, e.g. turbellarians, opisthobranch molluscs – and some pycnogonids.

The latter use their proboscis, jaws and pharyngeal pumps to suck polyps. In addition, the protonymphon larvae of a few species are released from the oviger of the adult males close to their hosts and, after they become attached, induce the formation of galls in which the larvae grow until they leave the hosts again for their predatory postlarval life that may occur on the previous “nursing colony” (e.g., Helfer & Schlottke 1935, Staples & Watson 1987, Chinery & Spooner 2001, Genzano 2002).

Here we report on laboratory observations and experiments on the relationships between the pycnogonid, *A. petiolatus* (Kröyer, 1844), and the hydrozoan, *H. echinata* Fleming, 1823, including the pycnogonid’s feeding and the polyps’ defence behaviour, *Hydractinia* polyps and *Anoplodactylus* pycnogonids (and Phoxichilidiidae or Anoplodactyidae in general) are classics of a sort as some of the first observations on pycnogonid-hydrozoan relationships were made on representatives of these taxa, e.g. Allman (1860), Wright (1863), Hallez (1905), Cole (1906), and Dogiel (1911). In these early studies, the facts of “feeding and galling” are presented, but descriptions of what happens while *A. petiolatus* visits *H. echinata* colonies are lacking. We therefore describe how *Anoplodactylus* and *Hydractinia* behave during such foraging trips. In addition, we investigate colonies under the influence of *A. petiolatus* using microscopical techniques, e.g., we show *A. petiolatus* larvae nested inside living polyps. A survey of *A. petiolatus* feeding on animals other than Cnidaria is given in Lotz (1968).
MATERIAL AND METHODS

In an aquarium with H. echinata settling on shells of the gastropod, Buccinum undatum, provided by the Biologische Anstalt Helgoland, A. petiolatus was found to be very abundant, both as larvae galling in H. echinata polyps and as free juveniles and adults. The animals were kept in artificial sea water at about 12°C. H. echinata was fed on brine shrimp larvae, Artemia salina. Pycnogonids were identified after King (1974) and Elliot et al. (1990).

Movement and feeding of about 30 A. petiolatus individuals of different sizes were observed for about 15 hours without any disturbance of the aquarium. All together about 50 foraging trips were observed during this period of time. In addition, pycnogonids were seized with forceps and released from about 10 cm above the hydrozoan colonies in such a way that they landed with body and legs in random positions (n=16).

Pictures of “gallzooids” with pycnogonid larvae were taken with a Zeiss Axioplan photomicroscope, surveys of A. petiolatus feeding on H. echinata with a conventional macro camera. SEM pictures were taken with a Leo 1430VP at 15 kV after fixation in AAF solution (85% ethanol, 10% acetic acid, 5% formalin; Anoplodactylus or 4% Glutaraldehyde in 0.1M sodium cacodylate buffer at pH 7.1 (Hydractinia), dehydration in a graded acetone series, CP-drying in a Bio Rad Polaron E 3000, and sputtering with gold in a Bio Rad SEM coating system.

RESULTS

General observations and “galling” of Hydractinia

In agreement with the above-cited earlier studies, our H. echinata colonies were food as well as larval habitat for A. petiolatus. SEM surveys of parts of H. echinata colonies previously visited by A. petiolatus allowed more detailed analysis of the effects of feeding (Fig. 1A): while trophozooids, dactylozooids and gonozooids showed no damage after A. petiolatus visits, the tips of the “spines”, i.e. the structures for which H. echinata is named, showed scar-like grooves and wrinkles apparently caused by pycnogonid proboscides. The habitus of an A. petiolatus individual mounted in foraging position is depicted in Fig. 1B. On the studied H. echinata colonies we observed numerous polyps transformed into long and slender “gallzooids” lacking tentacles, but having a swelling bearing a single A. petiolatus larva within the stomach cavity, as illustrated in the photographs showing vital polyps and larvae (Fig. 1D, E).

Undisturbed movement of A. petiolatus on the hydrozoan colonies and feeding

Mostly at night, A. petiolatus individuals left their hiding places under and/or within the Buccinum shells and moved slowly onto the H. echinata colonies. During this, polyps were not touched, i.e. the legs were set on the colony surface between the polyps, thus avoiding nematocyst attacks, and the body was also kept away from the colony’s surface (Fig. 1C, see also 1B).

Feeding took place in various locations on the colony, but one third to half of feeding observations were made at the tips of the spines standing between the normal trophozooids and nematozooids (Fig. 1A), thus corresponding well with the scars at the tips of spines seen on SEM preparations. Attacks on “gallzooids” containing pycnogonid larvae were not seen. For feeding, the pycnogonid bent down its forelegs and inserted the tip of the proboscis into the colony’s tissue. Afterwards it remained still for between 2 and 16 minutes while sucking the prey’s body fluid. Finally, it left the colony for its hiding place in the same stilted manner in which it had moved onto it.

Provoked contact between A. petiolatus and H. echinata

When pycnogonids were dropped onto H. echinata colonies, parts of the bodies of all tested animals came into contact with polyps. This led to massive reactions by H. echinata: polyps in reach of an A. petiolatus started to move towards the pycnogonid’s body and legs and apparently attacked it with nematocysts. Some polyps even tried to engorge legs or even whole pycnogonids (see below). However, all tested pycnogonids managed to withdraw from the colonies without any apparent serious bleeding. Using the claws at the tips of their legs as hooks, they brought themselves back to their normal upright walking position in a process that lasted between 1 and 10 minutes, and then moved on as described above.

Is Anoplodactylus “inedible” for Hydractinia?

Parts of the bodies of three of the smaller pycnogonids released over the colonies were engorged by polyps. Of one A. petiolatus only the distal halves of two legs were left outside the polyp, and the major part of the body was already in the gastric cavity. Remarkably, however, all three were able to withdraw from the polyp’s stomach by moving the free legs back and forth until they found a place to hook on with their claws and pull out the engorged part of the body. With the al-
most completely swallowed specimen this took about 2 hours, but was eventually successful.

**DISCUSSION**


Of interest, however, are some new points to be made regarding feeding behaviour and avoidance of the polyps’ defence. First, our observations indicate that – under the applied laboratory conditions – there seems to be a diurnal rhythm with a feeding peak at night and a resting and hiding phase during the day. It is, however, not clear whether this is also the pycnogonid’s behaviour in the natural habitat. *H. echinata* only grows on shells of *Buccinum*...
gastropods inhabited by hermit crabs like *Eupagurus bernhardus*. Hiding somewhere at or below the shell thus might help to avoid the loss of the prey colony when the crab actively moves around.

Secondly, *A. petiolatus* shows indications of an active avoidance of the colony’s defences by walking and sucking in a way that minimizes physical contact. Correspondingly, *Pycnogonum* sucks at the body stalk of *Metridium* and other sea anemones, where it is not within direct reach of the tentacles (*Helfer & Schlottke 1935*). If contact is provoked, however, it becomes evident that *Hydractinia* would defend itself against *Anoplodactylus* attacks – if the pycnogonid triggered such reactions. Except for the above-described scars, it is not clear at the moment to what extent *H. echinata* colonies are damaged by the pycnogonids as described by Mercier & Hamel (1994) for the sea anemone, *Bartholomea*.

Thirdly, our experiments indicate that *A. petiolatus* possesses a kind of immunity against *H. echinata* defences, as the pycnogonids were able to leave the colonies even after serious attacks. Most astonishing is the fact that they could even withdraw after being engaged. This might be connected to the larval development also taking place inside polyps, and hence the requirement for the larvae to move in and out of the polyp without becoming injured and staying inside for a longer period of time without being digested as seen in other endoparasitic forms (e.g. *Staples & Watson 1987*, *Lovely 1997*, Chinery & Spooner 2001). To make this point clear, comparisons with other arthropods engorged by polyps are necessary, as well as studies on the nesting of protonymphons.

In summary, *A. petiolatus* shows remarkable abilities to handle its host colonies relating to feeding, active defence avoidance, as well as a kind of passive immunity that might have contributed to the evolution of the unique galling of cnidarians by the larvae.

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**REFERENCES**


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